ACHLYA DeBARYANA HUMPHREY AND THE PROLIFERA GROUP

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(With Plate 78, Containing 13 Figures)

Achlya DeBaryana Humphrey is the *Achlya polyandra* of DeBary, *not* of Hildebrand, as Humphrey has shown;[1] and as Hildebrand's name is the older and applies to another plant, Humphrey's name should be used. Recent writers on the morphology of this species have ignored this and still call the plant *Achlya polyandra* DeBary. There are now recognized three very closely related species, forming what was called by Humphrey the *prolifera* group, which from the work of recent writers are becoming more and more difficult to separate. They are *Achlya prolifera* (Nees) DeBary, *A. DeBaryana* Humphrey, and *A. americana* Humphrey. Humphrey was himself aware of the very close resemblances of these species and remarked upon it; but on account of DeBary's assurance of the autonomy of the first two, felt called on to continue the distinction. According to DeBary,[2] *A. DeBaryana* (his *A. polyandra*) has antheridial branches that arise from the same main hyphae that bear the oögonia, and then branch and extend out to the oögonia on the branches from which they arose (which is most common) or to oögonia on other threads. In *A. prolifera,* on the other hand, he says that the antheridial branches are diclinous, always arising from other hyphae than the ones that bear the oögonia and that all oögonia are furnished with antheridia. He also says that while *A. prolifera* has oögonia with abundant pits, the oögonia of *A. DeBaryana* is without them. *Achlya americana* has antheridial branches that arise from the same hyphae as the oögonia, and it also has

[1] The Saprolegniaceae of the United States. Trans. Amer. Philos. Soc. 17: 1892.

[2] Untersuchungen über Peronosporeen und Saprolegnieen. Beitr. zur Morph. und Phys. der Pilze, IV Reihe. 1881.

abundantly pitted walls; thus uniting the characters of *A. prolifera* and *A. DeBaryana.*

From the work of Horn,[3] Peterson,[4] and myself it has now become evident that it is no longer possible to distinguish clearly between these species as established by DeBary and Humphrey. Forms are appearing constantly that combine their qualities in so confusing a manner that it is impossible to refer them with certainty. For example, Horn says (l. c., p. 224) that while the plant he describes is undoubtedly near *A. DeBaryana* (*A. polyandra* as he calls it), it cannot with absolute certainty be said to be identical with it; for while in *A. DeBaryana* the antheridia are mostly of androgynous origin, in his plant they are mostly diclinous. He also finds that when cultivated in peptone and in grape sugar or cane sugar certain oögonia show numerous pits.

In his work on Danish Fresh-water Phycomycetes, Peterson (l. c., p. 524) finds, of these three species, only *A. americana.* He places it as a form of *A. DeBaryana* (*A. polyandra,* as he calls it) not as a species, saying that "The reason I do not make use of Humphrey's species-name, but place this species as a variety of *Achlya polyandra* is that I am inclined to regard these pores as variable characters, as there are always some oögonia which have fewer pores than others."

Neither *Achlya prolifera* nor *A. DeBaryana* has so far been described from America. A form that is one or the other or both of these has appeared in my cultures at Chapel Hill for a number of years. It is by far the most abundant *Achlya* in our territory and may be had from springs, ditches and pools at any time of the year. During the spring and summer of this year (1912) I carefully studied the plant in pure cultures from a number of different collections.

To the naked eye, the species may be easily distinguished from others by the very large chlamydospores that usually make a white fringe at the periphery of the cultures. These are often arranged into groups that resemble the branching horns of a deer (fig. 1), or they may be shaped more like a section of *Halameda* (fig. 2). In mature cultures the hyphae become divided up

[3] Annales Mycologici 2: 207. 1904.
[4] Annales Mycologici 8: 294. 1910.

into sections containing dense protoplasm, each section being a chlamydospore. As with other chlamydospores, these will later either become sporangia or give off slender hyphae, sometimes many of them. Sometimes in their formation chlamydospores begin to break apart by bending backward as shown by the apical one in fig. 1. They rarely become entirely detached. The sporangia vary a great deal both in size and shape. At one extreme are those that are large and stout and rounded at the end, as in figs. 3 and 4, and at the other are long, slender forms that are drawn out to a narrow point, which is often bent, as in figs. 5 and 6.

In typical cases the spores on escaping act as usual in species of *Achlya,* forming a rather perfect sphere at the tip of the sporangium. Through long observation, however, cases have not rarely been seen where the spores fell apart to a greater or less degree, with the resultant formation of a community of detached groups, as shown in fig. 6. It is this variation from the usual course that led, fortunately, to the settlement of the uncertainty that has existed until now as to the presence or absence of a gelatinous matrix in the sporangium that is instrumental in causing the expulsion of the spores. I had long ago convinced myself of the existence of such a substance from the behavior of the spores in emerging in species of *Achlya* under usual and unusual conditions. The formation of a little emergence-papilla just before the escape, the rapidity and violence of the escape when followed by immediate quiescence (the sudden popping of a spore under constriction through a smaller opening would seem impossible under its own steam) and the frequent retention of some of the last spores in the sporangium are all strong evidence of mechanical propulsion under inside tension. And the presence of cilia on the escaping spores (a point that is still in dispute[5]) could scarcely modify the force of the evidence. The actual proof, however, of the presence of such a jelly was still lacking until presented under the conditions shown in fig. 6. If such a brotherhood of newly-emerged spores be disturbed, the *whole archipelago will move as a unit,* showing beyond a doubt that they are all bound together by a jelly that surrounds them. And it is the

[5] See Horn, L. C., p. 221.

swelling of this jelly that ejects the spores from the sporangium.[6]

Very often the spores do not come out, but either emerge through short individual tubes as in *Dictyuchus,* or sprout at once into hyphae as in *Aplanes.*[7] In fig. 7 the spores are emerging simply through holes; in fig. 8 they are escaping through tubes of considerable length. Some were seen in the act of escaping in both of these cases.[8] The passage of the protaplasm through the opening is at first very slow, but when about half way through the flow becomes much more rapid and the escape quickly follows. When free the spore scarcely shows any motion for several minutes, only a barely perceptible and uncertain rocking. Soon the motion becomes more active and in about five or ten minutes, depending on the temperature, the spore swims briskly away. In the case shown in fig. 7, the spores before emergence contained a good-sized vacuole. At the moment of complete emergence this vacuole became suddenly much smaller, probably by contracting and discharging as in the case of *Amoeba.* This was clearly discerned a number of times under the high power. The little depauperate sporangia shown in figs. 7 and 8 were formed immediately from spores sprouting in a large sporangium. When a small insect was placed near them, the end cell was sent out as a long and very delicate hypha that reached the insect and penetrated it. The spores in the sporangia were in a resting condition, but when deprived of air by being covered with a glass for a while, the spores began to emerge as shown. By this method sporangia of *Dictyuchus* and other species that have been resting for some time may be made to empty themselves whenever desired, as I have repeatedly demonstrated.

The oögonia are racemosely borne on straight or bent branches that vary greatly in length. Sometimes they are not one half as long as the diameter of the oögonia; again they may be four times as long. These extremes in length are rare and they usually vary from about one and one half to two and one half times the

[6] For Humphrey's argument against the mechanical expulsion of the spores in *Achlya,* see his Saprolegniaceae of the United States, page 66.

[7] Such variations occur in most of the species of Saprolegniaceae that I have studied. See Lechmere. The New Phytologist 9: 308. 1910; and 10: 167. 1911.

[8] This phenomenon was also observed for this species by Ward. See Quart. Journ. Micro. Scien. 23 N–S: *272.* 1883.

diameter of the oögonia. The walls of the oögonia are generally quite round and smooth, but at times they are furnished with low rounded projections at the pits, which are scarcely larger than to make the oögonia appear angular in section (fig. 9). In the walls of many oögonia pits are obviously present at pretty regular distances (fig. 10), but in many others the wall appears to be free of pits except that it is thin over the whole extent that is covered by the antheridia (fig. 11). Intercalary oögonia appear occasionally as shown in fig. 12. The oöspores are eccentric and are very variable in number. Two, four, and six are common numbers, one and eight are not rare, but more than eight are not often seen.

The antheridial branches arise from the same main hyphae as the oögonial branches. They usually extend for a considerable distance, branching either extensively or sparingly, and attach themselves to any oögonia they may meet, whether from their own main hyphae or from others. However, they seem to show some preference for the oögonia of other hyphae, and the antheridia on an oögonium are more apt to be of diclinous than of androgynous origin. This agrees with what Horn found in his plants, as mentioned above, and is contrary to DeBary's observations on his *Achlya polyandra* (*A. DeBaryana* Humphrey). In fig. 13 is shown an antheridial branch which has arisen by the proliferation of a halted oögonial initial, thus showing the essential homologies of the two sorts of organs. This branch has furnished antheridia for two oögonia of the same origin as itself. Not all oögonia are furnished with antheridia, the number without them varying from a small to a rather large proportion in different cultures.

It is now evident that our Chapel Hill form cannot certainly be referred to any described species of the *prolifera* group. If we compare their characters it would seem that our plant is somewhat nearer *A. prolifera* than it is to the others, as the antheridia are most often of diclinous origin, and the oögonia are generally pitted. But as *A. prolifera,* according to DeBary, does not have antheridia and oögonia on the same main hypha, that species is excluded here. And *A. DeBaryana* as described by DeBary (as *A. polyandra*) is equally excluded by its lack of oögonial pits and

the generally androgynous origin of its antheridia. However, from the figures of DeBary and Horn of *A. polyandra* DeBary (*A. DeBaryana* Humphrey), our plant seems really to be very near that species; and it seems best, at present, to extend somewhat the limits of *A. DeBaryana* so as to include Horn's form and our Chapel Hill plant.

Meanwhile, if *Achlya prolifera* can be found again, it should be carefully studied and the limits of its variation determined. If the other two are not distinct from it, then its name must be extended to all of them.

CHAPEL HILL, NORTH CAROLINA.

EXPLANATION OF PLATE LXXVIII

Fig. 1. A typical group of chlamydospores. × 75.

Fig. 2. Chlamydospores of another form. × 75.

Fig. 3. Several sporangia of the short, thick type. × 75.

Fig. 4. A sporangium opening by two tubes. × 75.

Fig. 5. Sporangia of a longer and narrower type. × 75.

Fig. 6. A sporangium like the above. The spores scattered somewhat on emerging. × 75.

Fig. 7. Depauperate sporangia formed from filaments sprouting directly from the spores in a large sporangium. Spores emerging from one filament. × 335.

Fig. 8. A sporangium similar to the above. × 335.

Fig. 9. An angular oögonium showing pits. × 335.

Fig. 10. A typical oögonium with pits; an antheridium attached; the contents of one egg filled in. × 335.

Fig. 11. An oögonium without pits except for the thin area where the antheridium is attached. Two antheridial tubes shown. × 335.

Fig. 12. Two oögonia, one intercalary, with diclinous antheridia. × 125.

Fig. 13. Three oögonia, with antheridial filament of androgynous origin × 125.